



TITLE:

Impacts of moso bamboo (*Phyllostachys pubescens*) invasion on dry matter and carbon and nitrogen stocks in a broad-leaved secondary forest located in Kyoto, western Japan

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2 **Impacts of moso bamboo (*Phyllostachys pubescens*) invasion on dry matter, and carbon and**
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Abstract

In western and central Japan, the expansion of exotic moso bamboo (*Phyllostachys pubescens* Mazel ex J. Houz.) populations into neighboring vegetation has become a serious problem. Although the effects of bamboo invasion on biodiversity have been well studied, shifts in nutrient stocks and cycling, which are fundamental for ecosystem functioning, are not fully understood. To explore the effects of *P. pubescens* invasion on ecosystem functions, we examined above- and belowground dry matter, and carbon (C) and nitrogen (N) stocks, in a pure broad-leaved tree stand, a pure bamboo stand, and two tree–bamboo mixed stands with different vegetation mix ratios in the secondary forest of Kyoto, western Japan. In the process of invasion, bamboo shoots offset broad-leaved tree deaths; thus, no clear trend was apparent in total above- or belowground biomass or in plant C and N stocks during invasion. However, the ratio of aboveground to belowground biomass (T/R ratio at the stand level) decreased with increasing bamboo dominance, especially in the early stages of invasion. This shift indicates that rapid bamboo rhizomatous growth is a main driver of substantial changes in stand structure. We also detected rises in the C/N ratio of forest-floor organic matter during bamboo invasion. Thus major impacts of *P. pubescens* invasion into broad-leaved forests include not only early shifts in biomass allocation, but also changes in the distribution pattern of C and N stored in plants and soil.

Keywords: allocation pattern, bamboo invasion, carbon and nitrogen stocks, *Phyllostachys pubescens*, stand structure.

39 **Introduction**

40

41 Moso bamboo (*Phyllostachys pubescens* Mazel ex J. Houz.), one of the largest bamboo species in
42 the world, was introduced from China into western Japan about 300 years ago for use as human food
43 (young sprouts) and other products (adult culms) (Suzuki 1978; Shibata 2003). The species has been
44 transplanted across a wide range of areas in western and central Japan, where well-managed
45 plantation forests were established. Since the 1980s, most of these forests have been abandoned due
46 to rapid declines in domestic bamboo industries.

47 Like other bamboo species, *P. pubescens* has active rhizomatous clonal growth. The
48 belowground rhizome system is leptomorphic; it grows laterally, allowing rapid, widespread
49 expansion of ramets (Makita 1998). Furthermore, young shoots quickly reach full heights of 10–20
50 m matching those of well-developed canopy trees. These growth capabilities probably facilitate
51 invasions of neighboring secondary broad-leaved forests and/or coniferous plantations, whereby the
52 bamboos rapidly become dominant components of the vegetation and often form pure stands in
53 previously deciduous or coniferous vegetation (Isagi & Torii 1998; Suzuki & Nakagoshi 2011;
54 Suzuki 2014). A clear risk of losing biodiversity and ecosystem functioning exists when exotic giant
55 bamboos establish near-monospecific stands in previously diverse woodlands. Studies are urgently
56 required to identify the relationships between growth characteristics of *P. pubescens*, its
57 overwhelming invasion impacts, and ecosystem functioning.

58 Many studies have reported losses of plant diversity following *P. pubescens* invasion (Nakai &

Kisanuki 2006; Zhang *et al.* 2010; Akutsu *et al.* 2012; Bai *et al.* 2013). However, few studies have reported on the effects of invasion on the sizes of carbon (C) and nitrogen (N) stocks or their cycling. Information on these parameters is crucial for better understanding of ecosystem functioning before and after invasion. However, data on the biogeochemical characteristics of pure bamboo forests are available. For example, Isagi *et al.* (1997) showed that values of gross production and belowground C allocation in *P. pubescens* stands are higher than those in temperate broad-leaved and/or coniferous forest stands. The canopy of *P. pubescens* forest has higher N contents (Li *et al.* 1998) and elevated transpiration rates (Komatsu *et al.* 2010) in comparison with broad-leaved and/or coniferous forest, suggesting that the canopy photosynthetic rate may be higher in *P. pubescens* stands than in native forest vegetation (Yen & Lee 2011). These characteristics are likely common to other bamboo species under various climatic conditions (Isagi 1994; Tripathi & Singh 1996; Tu *et al.* 2013).

Previous research on the impacts of bamboo invasions and/or range expansions on C and N biogeochemistry in Japan have focused on the understory dwarf species *Sasa kurilensis* (Rupr.) Makino & Shibata, which has growth traits similar to those of *P. pubescens* with the exception of culm height (Tripathi *et al.* 2005; Watanabe *et al.* 2013; Fukuzawa *et al.* 2014). These works have shown that *S. kurilensis* contributes greatly to C and N retention and their cycling in broad-leaved forest biomass and soils, but bamboo invasion and replacement of vegetation in native forests were not included in the scope of these studies.

Thus, our objective in this study was to describe the effects of invasion of giant bamboo, *P.*

pubescens, into secondary broad-leaved forest on (i) dry matter mass, (ii) C stocks, and (iii) N stocks in both plants and soils. We measured these parameters in above- and belowground plant parts, and in soil horizons of a secondary forest, in a pure *P. pubescens* stand, and in two mixed forest stands that differed in the degree of bamboo invasion.

Materials and methods

Study site

Fieldwork was conducted on Mt. Tennozan located on the boundary between Kyoto and Osaka prefectures in western Japan (34°54'N, 135°46'E; Fig. 1). Mean annual temperature and precipitation at the nearest weather station (AMeDAS) were 15.3°C (2001–2010, AMeDAS Kyotanabe, 34°50'N, 135°46'E) and 1459 mm (2001–2010, AMeDAS Nagaokakyo, 34°56'N, 135°41'E), respectively. The bedrock geology of our study area comprised Mesozoic sedimentary sandstone, shale, and chert belonging to Tamba terrane.

The native forest we studied was dominated by broad-leaved trees, including *Quercus serrata* Thunb. and *Quercus variabilis* Blume, which are typical of Japanese temperate secondary woodlands. *P. pubescens* was introduced a few hundred years ago in a patchy distribution pattern through the region. The stands were well managed for the production of young bamboo sprouts as

human food. Broad-leaved secondary forests were established and cut for fuel. Broad-leaved trees were harvested in our study area until the 1950s, but no anthropogenic disturbance has occurred for at least 60 years (Tokuchi *et al.* 2010). *P. pubescens* plantations in this region have been abandoned since the 1970s, and invading bamboo shoots were still expanding into neighboring broad-leaved forests at the time of our study (Torii & Isagi 1997; Torii 1998). According to a vegetation census by aerial photography in 2003, 46% of the areas around Mt. Tennozan (238.5 ha) are covered by secondary broad-leaved forests, 41% by *P. pubescens* stands, and 7% by mixed broad-leaved/bamboo stands (Tokuchi *et al.* 2010).

We selected vegetation stands dominated by (i) broad-leaved trees, (ii) *P. pubescens*, and (iii) mixed stands of trees and bamboo along a ridge located on Mt. Tennozan. We established one square plot (20 × 20 m) in broad-leaved tree forest stand (SF), one in a moso bamboo stand (BF), and two plots containing mixed forest stands (MF1, MF2). According to the earlier aerial photographs (1961, 1974, and 2003), BF had been dominated by *P. pubescens* prior to 1974. The bamboo has been invading MF1 since 1974 and MF2 since 1961. In plots MF1, MF2, and BF, expanding and overcrowding bamboo shoots have not been cut or managed during recent decades. Thus, plots SF, MF1, MF2, and BF represent a stage with no *P. pubescens* invasion, an early stage of invasion, a mid-stage of invasion, and a last stage of invasion, respectively.

Vegetation censuses and biomass estimation

119 We measured diameters at breast height (DBHs; cm) and identified all trees and bamboo shoots
120 exceeding 1 cm in DBH.

121 Above- and belowground biomasses of broad-leaved trees in all plots were estimated using
122 allometric equations relating DBH and height developed by different author earlier (Nishioka *et al.*
123 1982; Goto *et al.* 2006; Ogawa & Kira 1977; Nagano & Kira 1978; Ogino 1977). Broad-leaved tree
124 biomasses allocated to stems (main trunks, W_s ; kg), branches (W_b ; kg), and leaves (W_l ; kg) were
125 calculated thus:

$$126 \quad W_s = 0.02644 \times (\text{DBH}_{0.1}^2 \times H)^{0.9688} \quad (1)$$

$$127 \quad W_b = 0.01262 \times \text{DBH}_{0.1}^{2.364} \quad (2)$$

$$128 \quad W_l = 0.005921 \times \text{DBH}_{0.1}^{2.288}, \quad (3)$$

129 where H is tree height (m), which we estimated using the following relationship:

$$130 \quad 1/H = 1/(a \times \text{DBH}^b) + 1/H_{\max}, \quad (4)$$

131 where a and b are constants, and H_{\max} is the asymptotic maximum height (m; Ogawa & Kira 1977).

132 $\text{DBH}_{0.1}$ is stem diameter (cm) for a position located one-tenth of the way along the maximum trunk

133 length; $\text{DBH}_{0.1}$ was estimated from the measured DBH using the following empirical equation,

134 which was developed for a warm-temperate secondary oak forest by Nagano and Kira (1978):

$$135 \quad \text{DBH}_{0.1} = 0.941 \times \text{DBH} + 0.734. \quad (5)$$

136 We calculated the biomass of broad-leaved tree coarse roots (≥ 2 mm in diameter) (W_{below} ; kg)

137 using the following extended allometric equation:

$$138 \quad W_{\text{below}} = 0.082 \times \text{DBH}^2. \quad (6)$$

Eq. 6 was developed for a cool-temperate beech forest by Ogino (1977). We estimated the biomass of broad-leaved tree fine roots (<2 mm in diameter) by soil block sampling (see below).

To estimate the aboveground biomass of *P. pubescens* shoots, we applied the allometric equation developed for a site close to one of our study plots (BF) by Abe and Shibata (2009) in June 2006:

$$W = a \times \text{DBH}^b, \quad (7)$$

where parameters *a* and *b* were estimated individually for culms, branches, and leaves. The allometric relationship between the dry weight of each component and culm DBH was calculated separately for current-year shoots and shoots older than 1 year (Abe & Shibata 2009). The parameters are summarized in Table 1.

We used two methods of soil-block sampling to estimate the belowground biomass of *P. pubescens* shoots. One method estimated the “stump,” which we define here as the culm between the soil surface and rhizome (stump-block); the second method was used for root estimation (root-block). In the first procedure, we carefully excavated three soil blocks (each 50 × 50 cm to 50 cm depth) centered around bamboo shoots by using a shovel and saw within the pure *P. pubescens* stand located outside plot BF in August 2006. We cut free the aboveground part, dug into the soil, and carefully excavated the subterranean parts of the shoot. The stump-blocks were washed with tap water to remove mineral soils. The remaining root systems were separated into the stump and other components. The stumps were dried at 40°C for 1 week and then weighed. We constructed an allometric equation from the relationship between the dry weight of stump per shoot and culm DBH (see Eq. 7), and subsequently estimated the total bamboo stump biomass within our plots as a portion

159 of the belowground biomass components.

160 In the second procedure, we collected two soil blocks (50×50 cm to 30 cm depth) inside each
161 plot in the period from February to April 2006 for our calculations of root biomass per unit area and
162 the extent of bamboo rhizome lateral extension. These root-block samples were divided into vertical
163 portions 0–5, 5–10, 10–20, and 20–30 cm downward from the soil surface.

164 Within plots MF1, MF2, and BF, we found several centimeter-thick layers of live fine- and
165 coarse-roots between the mineral and organic layers (see below). We termed this layer the “root mat”
166 (RM) and separated it out from the other layers in the root-blocks. The living roots in the RM and
167 mineral soil layers were divided into those from broad-leaved trees and those from *P. pubescens*, and
168 sorted by hand into categories of fine roots, coarse roots, and bamboo rhizomes in the laboratory.
169 Each component was carefully separated according to illustrations in Suzuki (1978) and Makita
170 (1998). We distinguished rhizomes from roots by the presence of nodes in the former. The various
171 components were dried at 40°C for 72 h and weighed. The area-based biomasses of these
172 components were determined by calculation for these soil blocks.

173 Finally, we used the predictions of our allometric regressions for stand-level integration of the
174 biomasses of stems, branches, leaves, and coarse roots of broad-leaved trees, and the biomasses of
175 culms, branches, leaves, and stumps of *P. pubescens*. We used the root-block predictions to integrate
176 area-based biomasses of tree fine roots, and bamboo coarse roots, fine roots, and rhizomes in the RM
177 and mineral soil layers.

178

179 *Soil sampling*

180

181 We estimated the dry masses of organic matter in the organic soil layers of the four plots. Four
182 frames (20 × 20 cm) were deployed haphazardly on the surface soils in the period February–April
183 2006, and from these, we collected all forest-floor organic matter in the litter (Oi) and humus layers
184 (Oe+Oa). Samples of this organic matter were dried at 40°C for 1 week and weighed.

185 We used soils collected in the root-blocks to determine soil bulk density. After removing roots
186 and rhizomes, we divided the dry weight of fine mineral soil that passed through a 2-mm sieve by
187 the total dry weight of bulk soil for each soil layer. Organic matter and mineral soils were also
188 present in the RM layer. Consequently, we used a 4-mm mesh to sieve the RM samples collected
189 from the root-blocks in preparation for soil analysis.

190

191 *Chemical analysis*

192

193 Bamboo organs (leaves, branches, culms, fine and coarse roots, and rhizomes), forest-floor organic
194 matter, and mineral soils were ground in a mill prior to measurements of C and N contents with a
195 NC analyzer (NC-22A; Sumigraph, Osaka, Japan). We assumed that the C and N contents of
196 bamboo stumps were the same as those in bamboo rhizomes. Reports have indicated that the C and
197 N contents of *P. pubescens* leaves vary significantly by culm age (Li *et al.* 1998). Thus, we made
198 separate measurements of aboveground compartments of *P. pubescens* on current-year shoots and

those older than 1 year. We obtained C and N contents of most broad-leaved tree organs from previous reports (Tsutsumi *et al.* 1968; Katagiri & Tsutsumi 1975), but our data on fine and coarse roots were obtained by the analyses described above. By multiplying the dry weights of plant organs or soil organic matter in the soil layers by the respective C and N contents and summing, we were able to estimate the total area-based C and N stocks in each plot.

Data analysis

We used paired *t*-tests to detect significant differences in the C and N contents of *P. pubescens* leaves, branches, and culms between current-year shoots and those older than 1 year. The Kruskal-Wallis test was used to test the effect of stand characteristics on the mean C and N contents in coarse and fine roots of bamboo and broad-leaved trees, and in bamboo rhizomes and stumps. We also used the Stell-Dwass post hoc test for multiple comparisons to detect differences in the mean C and N contents in these components between pairs of stand types. Significant differences in the mean C and N contents in the soil organic matter within each layer (forest floor, RM, and 0–10-cm and 10–30-cm layers) among stand types were also analyzed by the Kruskal-Wallis test followed by the Steel-Dwass post hoc test. Statistical analyses were performed using R software (R Development Core Team 2010).

219 **Results**

220

221 *Stand structure*

222

223 Stem and culm densities, mean DBH, total basal area (BA), proportion of *P. pubescens* in BA,
224 numbers of species, and dominant broad-leaved tree species in SF, MF1, MF2, and BF are
225 summarized in Table 2. As the proportions of *P. pubescens* in BA increased, the numbers of plant
226 species in the plots decreased (Table 2). Patterns of DBH frequency distribution differed
227 dramatically among plots (Fig. 2). Thus, DBH distributions of broad-leaved trees were positively
228 skewed in plots SF, MF1, and MF2, while DBH distributions of bamboo shoots showed a normal
229 curve in plots MF1, MF2, and BF. In mixed stands (plots MF1 and MF2), distributions showed a
230 bimodal curve with one smaller mode comprising the DBH distribution of broad-leaved trees and the
231 larger mode comprising that of bamboo shoots. Mean DBH values of bamboo culms were similar
232 among the plots regardless of differences in culm density (Table 2). As bamboo culm densities
233 increased, the frequencies of broad-leaved trees with DBH values <12 cm decreased dramatically
234 (e.g., in plot MF2); we found no trees with DBH values >12 cm in plot BF (Fig. 2).

235

236 *Above- and belowground biomasses*

237

238 We used an allometric equation (Eq. 7) describing the relationship between culm DBH and stump

dry weight to predict biomasses of belowground stumps of *P. pubescens* shoots; the calculated values of parameters a and b were 7.71×10^{-2} and 1.434 ($r^2 = 0.954$), respectively.

Figure 3 depicts the vertical distribution of belowground biomasses of coarse and fine roots, and rhizomes of *P. pubescens* shoots per unit area in plots MF1, MF2, and BF. Fine roots of *P. pubescens* occurred most densely in the 0–5-cm mineral soil layer; coarse roots and rhizomes occurred most densely below 5 cm soil depth (Fig. 3).

Details of aboveground and belowground biomasses of each compartment, and total biomasses are presented in Fig. 4 and Appendix A. No increasing or decreasing trends were observed in aboveground and total biomasses. However, belowground biomass increases were associated with *P. pubescens* invasions (Fig. 4). At the stand level, the dry mass ratio of non-photosynthetic organs to photosynthetic organs (culm/foilage ratio, C/F; Iwaki 1958) increased from 22.7 to 35.8 (Fig. 5a), while the dry mass ratio of aboveground organs to belowground organs (top/root ratio, T/R) decreased from 3.41 to 1.39 as the proportion of bamboo increased in BA (Fig. 5b). The C/F ratio of broad-leaved trees remained constant among plots other than BF (Fig. 5a), in which all large canopy trees had disappeared as a result of the bamboo invasion (Fig. 2). No differences were detected in the C/F ratio of *P. pubescens* shoots across our plots (Fig. 5a). Among plots, the T/R ratio of broad-leaved trees was lowest in BF; the T/R ratio of *P. pubescens* tended to increase with increasing proportions of bamboo in BA (Fig. 5b).

Organic matter mass at the forest floor level and the bulk density of mineral soil

259

260 Values of forest-floor organic matter mass in the Oi layer were not significantly different among
261 plots (Kruskal-Wallis test, $P > 0.05$), but those in the Oe+Oa layer were significantly larger in plot
262 SF than in the other plots (Kruskal-Wallis and Steel-Dwass tests, $P < 0.05$; Table 3).

263 The bulk density of mineral soil that passed through a 2-mm sieve tended to increase with depth
264 and decrease with the proportion of bamboo in BA (Table 4). The RM layer, which appeared to have
265 developed between the organic and the mineral soil layers in the presence of *P. pubescens*, included
266 a small amount of mineral soil (Table 4).

267

268 *C and N contents and stocks in plants and soils*

269

270 Details of the mean C and N contents in each compartment of *P. pubescens* and broad-leaved trees
271 are listed in Table 5. In *P. pubescens*, the C contents in leaves, branches, and culms were not
272 significantly different between current shoots and shoots older than 1 year (paired *t*-test, $P > 0.05$;
273 Table 5), and the N contents in leaves, branches, and culms did not vary between the two age classes
274 of shoots (paired *t*-test, $P > 0.05$; Table 5). The leaves and the branches of *P. pubescens* contained
275 less C and more N than equivalent organs of broad-leaved trees. The culms of *P. pubescens*
276 contained less C than the stems of broad-leaved trees; the N contents in bamboo culms and tree
277 stems were closely similar (Table 5). The coarse and fine roots of *P. pubescens* contained less C and
278 N than those of the broad-leaved trees (Table 5). C and N contents in the rhizomes, stumps, and

coarse roots of *P. pubescens* were closely similar.

C and N contents of each soil layer in the four plots are detailed in Table 6. C and N contents in the Oi layer differed significantly among plots (Kruskal-Wallis and Steel-Dwass tests, $P < 0.05$). As the proportion of bamboo BA increased in the stands, the C and N contents in this layer decreased (Table 6).

Values of C stocks in plants and soils in the stands ranged from 83.4 to 108.2 MgC ha⁻¹ in aboveground parts, from 28.7 to 64.6 MgC ha⁻¹ in belowground parts, and from 45.0 to 54.0 MgC ha⁻¹ in soils (Fig. 6a, Appendix B). The values of N stocks ranged from 0.44 to 0.57 MgN ha⁻¹ in aboveground parts, from 0.38 to 0.60 MgN ha⁻¹ in belowground parts, and from 2.13 to 2.98 MgN ha⁻¹ in soils (Fig. 6b). Forty to sixty percent of C was stored in aboveground parts, but >70% of the stand N stock was stored in the soils (Fig. 7). The proportion of total stand C stored in belowground parts increased with increasing proportions of bamboo BA, but the proportions of N shifted little in response to increasing bamboo BA (Fig. 7).

Discussion

Stand structure and biomass in vegetation dominated by broad-leaved trees and bamboo

The dominant tree species in our stands were *Q. serrata* and/or *Q. variabilis*, which are typical of the

secondary forest around Mt. Tennozan (Table 2). The above- and belowground biomasses in a pure stand of broad-leaved trees (SF) were 211.8 and 62.1 Mg ha⁻¹, respectively (Fig. 4, Appendix A); these values exceed those previously reported for forests with similar tree species composition in the other areas (Table 7). The differences between studies is likely attributable the greater stand age (~60 years) and a higher density of trees with DBH >5 cm in our data set. Surviving large trees with DBH values exceeding 30 cm on Mt. Tennozan also contributed significantly to the large biomass values we calculated.

Culm density (9675 ha⁻¹; Table 2) and aboveground biomass (182.1 Mg ha⁻¹; Fig. 4, Appendix A) in the abandoned pure *P. pubescens* stand (BF) were within the range of previously reported values for equivalent vegetation, but belowground biomass we measured (127.1 Mg ha⁻¹; Fig. 4, Appendix A) exceeded previously reported values (Table 8). *P. pubescens* biomass surveys in various regions of Japan have detected an exponential relationship between BA and above- or belowground biomasses (FFPRI 2009). Using this regression relationship, we calculated biomasses in our *P. pubescens* stand (BA = 88.3 m² ha⁻¹; Table 2) of 181.2 Mg ha⁻¹ above ground and 91.4 Mg ha⁻¹ below ground, which fit our empirical estimates for aboveground biomass but not those for belowground biomass. The discrepancy between estimates is likely due to the difficulty in accurately defining the belowground compartment of bamboo species, especially for the leptomorph types like *P. pubescens*. Comprehensive inclusion of all belowground compartments requires estimation of the spatial extent of rhizome and root system biomasses in addition to stump estimates derived from the allometric relationship with DBH. Previous studies may not have implemented this inclusive

procedure and therefore underestimated belowground biomass. We believe that our comprehensive approach provides reliable values.

We calculated T/R values of 3.41 and 1.39 in the secondary broad-leaved (SF) and *P. pubescens* stands (BF; Fig. 5b), respectively. According to Saito (1989), T/R falls within the range of 3–7 and is close to unity in broad-leaved/coniferous forest stands and grasslands. Thus, our measure of stand structure in *P. pubescens* vegetation was close to that of grassland meadows, but bamboo biomass was comparable to that of a well-developed secondary forest.

Changes in stand structure and biomass as bamboo invasion proceeds

In our study sites, bamboo density and percentage of bamboo in total BA was higher in the plot where the number of years passed after *P. pubescens* invasion was longer (Table 2), indicating that the dominance of *P. pubescens* in the plot represents a stage of invasion.

As *P. pubescens* invaded our secondary forest sites, numbers of plant species decreased and total basal area increased. Okutomi *et al.* (1996) observed similar shifts in the vegetation during a study of plant spatial distributions and canopy structures in a mixed broad-leaved tree/bamboo forest, although they did not determine biomasses. At our study site, the above- and belowground biomasses of broad-leaved trees decreased as those of *P. pubescens* increased, but no monotonous trends were apparent in the summed biomass data (Table 5c). These relationships might be explainable as follows. In the early stages of invasion, smaller trees are replaced by small numbers

of bamboo culms, with consequent decreases in whole stand biomass (plot MF1). Only large trees survive as the invasion proceeds. During the mid-stages of the invasion process, bamboo density increases and stand biomass reaches a maximum (as in plot MF2). Finally, whole stand biomass decreases when high densities of bamboo cause the deaths of large broad-leaved trees (perhaps due to competition for light, water, and/or mineral nutrients), as in plot BF.

An increase in the C/F ratio as bamboo dominance increased indicates that the proportion of photosynthetic organs in the aboveground biomass increased at the stand level (Fig. 5a). *P. pubescens* is a highly productive plant that produces more leaves on fewer culms (stems) than woody species (Isagi *et al.* 1997; Yen & Lee 2011). In addition, the leaf N contents of *P. pubescens* exceeded those of woody plants (Table 5, Li *et al.* 1998), suggesting that *P. pubescens* has a higher photosynthetic capacity (Reich *et al.* 1997). Isagi *et al.* (1997) measured high gross production rates in a *P. pubescens* stand. They also pointed out that a large proportion of the photosynthetic products was allocated to belowground systems and then transported to newly developing bamboo shoots (Isagi *et al.* 1997).

In stands where bamboo had invaded secondary forest (plots MF1 and MF2), the belowground biomass of *P. pubescens* exceeded aboveground biomass (Fig. 4c, Appendix A), and the stand T/R ratio declined dramatically (Fig. 5b). These trends indicate that the ramet population of *P. pubescens* initially expands its root system into adjacent forest stands, a process that results in rapid changes in stand biomass distribution.

359 *Changes in C and N stocks in forest stands following bamboo invasion*

360

361 Although aboveground compartments of *P. pubescens* had lower C and higher N contents than those
362 of broad-leaved trees (Table 5), total aboveground C and N stocks did not change monotonically
363 following *P. pubescens* invasion of secondary forest stands (Fig. 6) due to an aboveground biomass
364 buildup during invasion. The C and N contents in the belowground compartments of broad-leaved
365 trees exceeded those of bamboo (Table 5). C stocks per unit area in belowground compartments and
366 total belowground biomass approximately doubled during *P. pubescens* invasions (Fig. 6a, Appendix
367 B), but N stocks did not change (Fig. 6b, Appendix B). This indicates that the difference of not only
368 the dry matter mass but also the chemical content of each plant compartment between broad-leaved
369 tree and *P. pubescens* can largely affect the element stock and distribution in the forest stand. These
370 physiological characteristics of *P. pubescens* including higher productivity, greater belowground
371 allocation, and lower C and/or higher N contents in leaves rather than those of trees are partly
372 reported in cases of some other bamboo species, such as *P. bambusoides* Sieb. et Zucc. in western
373 Japan (Isagi *et al.* 1993), *Bambusa* spp. in Puerto Lico (O'Connor *et al.* 2000), and *Dendrocalamus*
374 *strictus* (Roxb.) Nees in India (Tripathi & Singh 1996). Because these studies only described the
375 stand structure and/or nutrient dynamics in bamboo forest, further researches are necessary to
376 elucidate their changes by bamboo invasion into the native forest in each area.

377 When total values were calculated by summing the stocks for plants and soil organic matter in
378 each plot, the ratio of belowground C in total C stocks increased during bamboo invasion of

secondary forest (Fig. 7a). Thus, the development of *P. pubescens* root systems may greatly change the C distribution in forest stands.

More than 70% of N was stored in the soils (Fig. 7b). In general, microbial decomposition of organic matter in forest soils releases C as gaseous CO₂ into the atmosphere, but N is largely immobilized and retained underground (e.g., Vitousek et al. 1979; Johnson *et al.* 2000; Berg & McLaugherty 2014). This results in little effect of invasions by *P. pubescens* on N stock size or its distribution.

The C/N ratio of organic matter in the surface soil layer (on a weight basis) is a useful indicator of the degree of decomposition (Berg & McLaugherty 2014), net nitrification rate (Goodale & Aber 2001; Fukushima *et al.* 2011) and leaching of mineralized N from forest soils (Lovett *et al.* 2004). When forest-floor organic matter with a relatively high C/N ratio decomposes, organic N is generally mineralized but then rapidly immobilized by heterotrophic soil microbes. When the C/N ratio of soil organic matters decreases as decomposition progresses, microbe demand for mineral N becomes satiated; inorganic N is then nitrified by autotrophic nitrifiers and subsequently leached from the soil. The C/N ratio of the forest-floor organic matter at our study site increased monotonically with bamboo shoot density (Table 9). Previous studies revealed that understory dwarf bamboo like *S. kurilensis* in a broad-leaved secondary forest in northern Japan (Tripathi *et al.* 2005; Watanabe *et al.* 2013) and *Chusquea culeou* E. Desv. in an old-growth broad-leaved forest in Patagonia (Austin & Marchesini 2012) plays a key role in retaining mineral N in soil through N uptake by bamboo and N immobilization during bamboo litter decomposition. The giant bamboo has greater biomass, litter

fall, and productivity than dwarf bamboo. Hence, the process of *P. pubescens* invasion into secondary forest may depress the rate of N cycling and prevent the loss of inorganic N from soils.

Moreover, Umemura & Takenaka (2014a) demonstrated that soil pH increases as *P. pubescens* invades surrounding evergreen coniferous forests, which may greatly affect the net nitrification rates in soil because some groups of ammonia-oxidizing bacteria can deactivate and some groups of ammonia-oxidizing archaea can activate under low pH (Nicol *et al.* 2008). Overall, *P. pubescens* invasion into forest stands clearly alters N cycling between plants and soil due to changes in soil organic matter quality (e.g., the C/N ratio) and physicochemical parameters (e.g., pH). The details of these processes should be studied by examining changes in soil N dynamics during invasion.

Conclusion

In our secondary forest located in western Japan, stand structure and the distribution of plant biomass were affected by *P. pubescens* dominance, which is almost equal to the degree of *P. pubescens* invasion. The changes in (i) standing biomass, (ii) C and N stocks in plants and soil, and (iii) their distributions during bamboo invasion were likely triggered by the rapid bamboo rhizomatous clonal growth and the deaths of large(L412-414) broad-leaved trees. Nevertheless, few differences in biomass or C and N stock sizes were observed between a broad-leaved forest stand and a pure *P. pubescens* stand, suggesting that the capabilities for storing C and N in plants and soil

are comparable in broad-leaved and bamboo forests. In contrast, the allocation of C into belowground biomass (T/R ratio), the N content of leaves, the C/F ratio in aboveground vegetation, and the C/N ratio in forest-floor organic matter shifted markedly in response to invasion. These shifts are likely driven by the physiological attributes of invading *P. pubescens*, and may have large effects on the rates of C and N cycling and loss in forest ecosystems during early invasion. To better understand the effects of *P. pubescens* invasion on ecosystem functions, future studies on soil N dynamics and N retention will be required.

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600

601 **Table 1.** The parameters of regression equations predicting biomasses of each *P. pubescens* organ
602 from diameters at breast height (DBH). Data are from Abe and Shibata (2009).

603

		a	b	n	r^2
Leaf	Current year	1.149×10^{-2}	1.515	7	0.853
	≥ 1 year	4.774×10^{-3}	1.976	8	0.851
Branch	Current year	1.045×10^{-1}	1.185	7	0.722
	≥ 1 year	4.647×10^{-2}	1.483	8	0.74
Culm	Current year	6.210×10^{-2}	2.261	7	0.951
	≥ 1 year	1.305×10^{-1}	2.052	8	0.915

604

605

606 **Table 2** Densities of broad-leaved tree stems and bamboo shoots, mean diameter at breast height (DBH) of broad-leaved trees and bamboo shoots, total basal
607 area (BA), proportion of bamboo in BA, number of plant species, and dominant tree species in our study plots.

Plot	Stem density (No. ha ⁻¹)	Culm density (No. ha ⁻¹)	Mean DBH of woody trees (cm)	Mean DBH of bamboos (cm)	Total BA (m ² ha ⁻¹) ^a	Percentage of bamboo in BA (%)	Number of Species (No. plot ⁻¹)	Dominant tree species ^b
SF	6600	0	7.29	n.a.	52.9	0	19	<i>Quercus serrata</i> (19.3), <i>Myrica rubra</i> (19.0), <i>Q. variabilis</i> (15.1), <i>Ilex pedunculosa</i> (12.3)
MF1	6225	1275	5.88	10.03	46.1	20.0	17	<i>Q. serrata</i> (27.2), <i>I. pedunculosa</i> (22.9), <i>Chamaecyparis obtusa</i> (16.8)
MF2	2375	5575	7.28	10.51	76.1	69.1	14	<i>Q. variabilis</i> (18.3), <i>Q. serrata</i> (5.4), <i>Q. glauca</i> (4.0)
BF	150	9675	1.97	10.52	88.3	99.9	4	

^a Total basal area (BA) at the breast height

^b Order of relative dominant woody tree species was based on BA. Percent of total BA in parentheses.

DBH; diameter at the breast height

n.a.; not available

608

609 **Table 3** Mean dry weights of organic matter in the Oi and Oe+Oa soil layers ($n = 4$). SD in
610 parentheses.

611

Layer	SF		MF1		MF2		BF	
Oi (Mg ha ⁻¹)	4.05	(0.767)	4.08	(0.874)	5.25	(2.32)	3.47	(1.69)
Oe+Oa (Mg ha ⁻¹)	20.6	(6.05) <i>a</i>	1.89	(0.598) <i>b</i>	1.4	(0.984) <i>b</i>	1.53	(0.291) <i>b</i>

612 Different letters (*a*, *b*) indicate significant differences among plots ($P < 0.05$, Kruskal-Wallis test
613 followed by Steel-Dwass post hoc test).

614

615 **Table 4** Mean soil bulk density in the root mat and mineral soil layers ($n = 2$).

Layer	SF	MF1	MF2	BF
RM (Mg ha ⁻¹)	n.a.	19.3	14.8	19.2
0-5cm (Mg ha ⁻¹)	462.6	360	314.5	241.8
5-10cm (Mg ha ⁻¹)	534.8	373.6	403.2	263.6
10-20cm (Mg ha ⁻¹)	937.3	901.2	798	640.9
20-30cm (Mg ha ⁻¹)	919.3	760.5	658.8	821.5

616 n.a.; not available

617

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619

620 **Table 5** Mean C and N contents in each organ of *P. pubescens* and broad-leaved trees. SD in
621 parentheses. Both C and N contents in leaves, branches, and culms of bamboo shoots were not
622 significantly different between current shoots and shoots older than 1 year (paired *t*-test, $P > 0.05$).

		Total C (%)		Total N (%)		<i>n</i>
<i>Phyllostachys pubescens</i>						
Leaf	Current	41.9	(1.72)	2.43	(0.30)	3
	≥ 1 year	43.2	(0.46)	2.03	(0.19)	3
Branch	Current	46.4	(0.23)	0.55	(0.17)	3
	≥ 1 year	45.8	(1.11)	0.51	(0.25)	3
Culm	Current	46.3	(0.69)	0.18	(0.043)	3
	≥ 1 year	46.8	(1.22)	0.19	(0.050)	3
Coarse root		44.2	(0.32)	0.23	(0.015)	9
Fine root		43.2	(0.50)	0.51	(0.044)	9
Rhizome and stump		44.3	(0.15)	0.26	(0.029)	9
<i>Broad-leaved tree</i>						
Leaf		52.6	†	1.57	‡	
Branch		51.8	†	0.38	‡	
Stem		50.9	†	0.19	‡	
Coarse root		46.1	(0.48)	0.59	(0.049)	9
Fine root		46.7	(0.54)	0.77	(0.040)	8

623 †; Data are from Katagiri and Tsutsumi (1975). ‡; Data are from Tsutsumi *et al.* (1968).

624 **Table 6** Mean C and N contents in soil organic matter in each soil layer. SD in parentheses ($n = 5$).

	Soil layer	SF		MF1		MF2		BF	
C(%)	Oi	46.2	(0.36) <i>a</i>	45.6	(0.68) <i>ab</i>	43.5	(0.95) <i>b</i>	39.8	(0.59) <i>c</i>
	Oe+Oa	28.7	(7.91)	27.7	(10.1)	39.3	(2.86)	31.5	(4.29)
	RM	n.a.		28.7	(10.1)	26.6	(8.99)	22.9	(7.64)
	0-10 cm	2.92	(0.99)	3.44	(0.946)	3.25	(1.68)	3.34	(0.86)
	10-30 cm	0.69	(0.13)	0.71	(0.13)	1.57	(0.87)	2.11	(0.46)
N(%)	Oi	1.02	(0.17) <i>a</i>	0.99	(0.073) <i>a</i>	0.85	(0.17) <i>ab</i>	0.64	(0.11) <i>b</i>
	Oe+Oa	1.59	(0.21)	1.22	(0.41)	1.61	(0.14)	1.35	(0.13)
	RM	n.a.		1.22	(0.33)	1.36	(0.50)	1.21	(0.38)
	0-10 cm	0.16	(0.058)	0.16	(0.045)	0.18	(0.088)	0.22	(0.039)
	10-30 cm	0.042	(0.001)	0.041	(0.006)	0.099	(0.041)	0.11	(0.014)

625 Different letters (*a*, *b*, *c*) indicate significant differences among plots ($P < 0.05$, Kruskal-Wallis test followed by Steel-Dwass post hoc test).

626 RM; root mat layer. n.a.; not available.

627

628 **Table 7.** Above- and belowground biomass in *Quercus serrata* secondary forest from previous studies and this study.

Site	Age (year)	Aboveground biomass (Mg ha ⁻¹)	Belowground biomass (Mg ha ⁻¹)	Reference
Shimane Prefecture	40	96.3 - 218.0	n.a.	Katagiri (1988)
Kyoto Prefecture	n.a.	102	23.4	Goto <i>et al.</i> (2003); Dannoura <i>et al.</i> (2006)
Okayama Prefecture	58 - 61	79.2 - 161.3	n.a.	Goto <i>et al.</i> (2006)
Miyazaki Prefecture	60 - 62	118.5 - 127.4	n.a.	Kai (1984)
Iwate Prefecture	36	131.1	n.a.	Segawa and Kato (1970)
Nagano Prefecture	16	132.2	24.1	Katakura <i>et al.</i> (2007)
Toyama Prefecture	33 - 35	114.8 - 206.8	n.a.	Hasegawa (1989)
Kyoto Prefecture	60 ~	211.8	62.1	This study (plot SF)

629 n.a.; not available.

630

631 **Table 8.** Above- and belowground biomass in un-managed *Phyllostachys pubescens* forest from previous studies and this study.

632

Site	Culm density (shoots ha ⁻¹)	Aboveground biomass (Mg ha ⁻¹)	Belowground biomass (Mg ha ⁻¹)	Reference
Kagoshima Prefecture	5000 - 6130	82.8 - 146.6	n.a.	Kumemura <i>et al.</i> (2009)
Kyoto Prefecture	7700	137.9	44.6	Isagi <i>et al.</i> (1997)
Central Taiwan	6996 - 7188	81.6 - 96.8	n.a.	Yen and Lee (2011)
Kyoto Prefecture	7967 - 8300	217 - 224	n.a.	Abe and Shibata (2009)
Aichi Prefecture	2400 - 4790	31.4 - 107	36 - 67.5	Umemura and Takenaka (2014b)
Gifu Prefecture	8125 - 16300	42.1 - 83.5	89.1 - 98.5	Goto <i>et al.</i> (2008)
Kyoto Prefecture	9675	182.1	127.1	This study (plot BF)

633 n.a.; not available

634 **Table 9** C/N ratios of aboveground and belowground compartments and soil layers, their respective
635 subtotals, and total values.

		SF	MF1	MF2	BF
Aboveground	Leaf	33.5	32.3	27.6	21.2
	Branch	136.3	130.7	111.8	89.4
	Stem and Culm	268.6	265.8	256.9	246.8
	<i>Subtotal</i>	189.7	187.3	182.3	174.9
Belowground	Coarse root	78.4	93.7	121.9	192.7
	Fine root	60.9	81.2	84.8	85.4
	Rhizome	n.a.	169.2	169.2	169.2
	Stump	n.a.	169.2	169.2	169.2
	<i>Subtotal</i>	75.9	97.2	107.0	132.9
Soil	Oi layer	45.4	45.9	51.3	62.1
	Oe+Oa layer	18.1	22.8	24.4	23.4
	Root mat layer	n.a.	23.6	19.5	19.0
	0-10 cm	17.8	21.9	18.3	15.3
	10-30 cm	16.7	17.5	15.9	19.6
	<i>Subtotal</i>	17.9	21.2	17.7	18.3
<i>Total</i>		50.2	56.2	53.0	50.4

636 n.a.; not available.

637 Figure legends

638

639 **Fig. 1** Location of the study site.

640

641 **Fig. 2** Diameter at breast height (DBH) frequency distributions of *P. pubescens* (■) and other plants
642 (□) in the study plots: (a) plot dominated by secondary broad-leaved forest (SF), (b) mixed
643 bamboo/broad-leaved forest plot subjected to bamboo invasion since 1974 (MF1), (c) mixed
644 bamboo/broad-leaved forest plot subjected to bamboo invasion since 1961 (MF2), (d) plot
645 dominated by bamboo (BF).

646

647 **Fig. 3** Vertical distributions of biomass in *P. pubescens* roots ($n = 2$ for the root mat layer, $n = 4$ for
648 each mineral soil layer in the 0–30 cm depth range, and $n = 2$ for rhizomes). Error bars are standard
649 deviation (SDs).

650 * RM; root mat

651

652 **Fig. 4** (a) Aboveground and (b) belowground biomasses of broad-leaved trees and *P. pubescens*
653 organs; (c) total biomass.

654

655 **Fig. 5** (a) Ratios of non-photosynthetic organ to photosynthetic organ dry weights (C/F); (b) ratios of
656 aerial organ to root dry weights (T/R) for whole plants, broad-leaved trees, and *P. pubescens*.

657

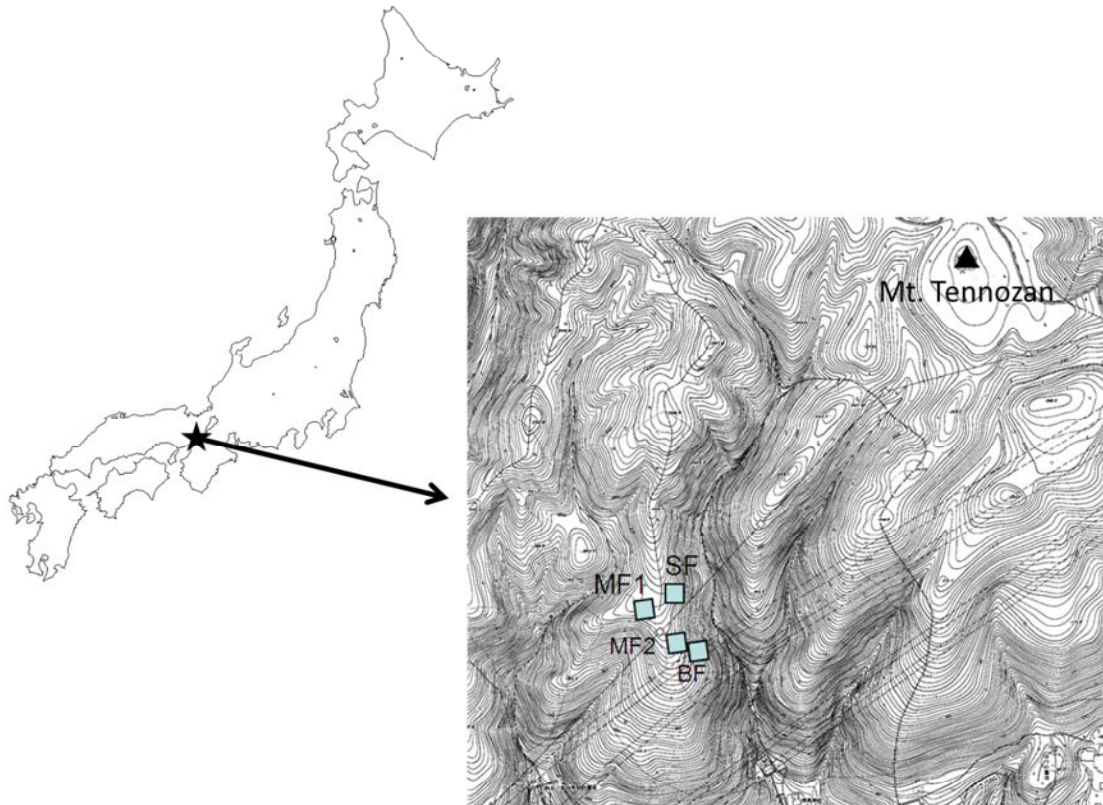
658 **Fig. 6** (a) Carbon and (b) nitrogen stocks in all aboveground and belowground compartments and in
659 each soil layer.

660

661 **Fig. 7** The proportion of above- and belowground compartments and soils to total (a) carbon and (b)
662 nitrogen stocks for four plots.

663

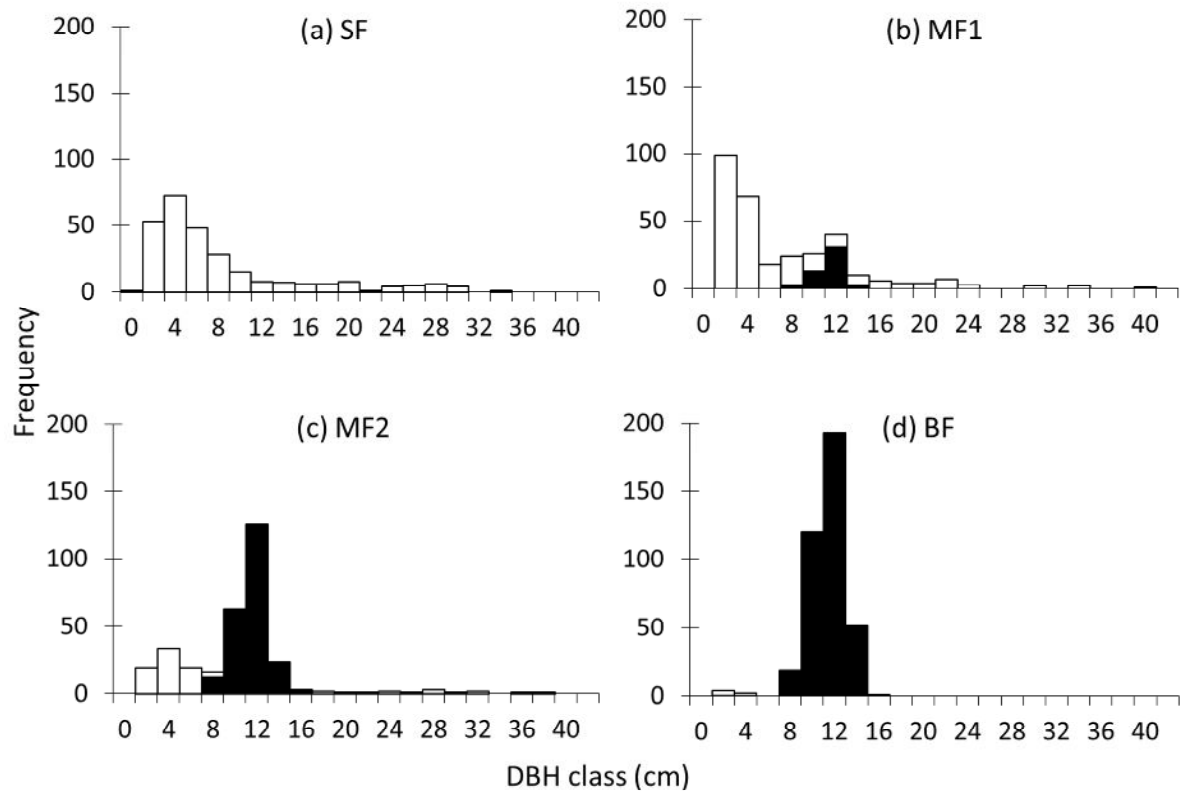
664 Fig. 1



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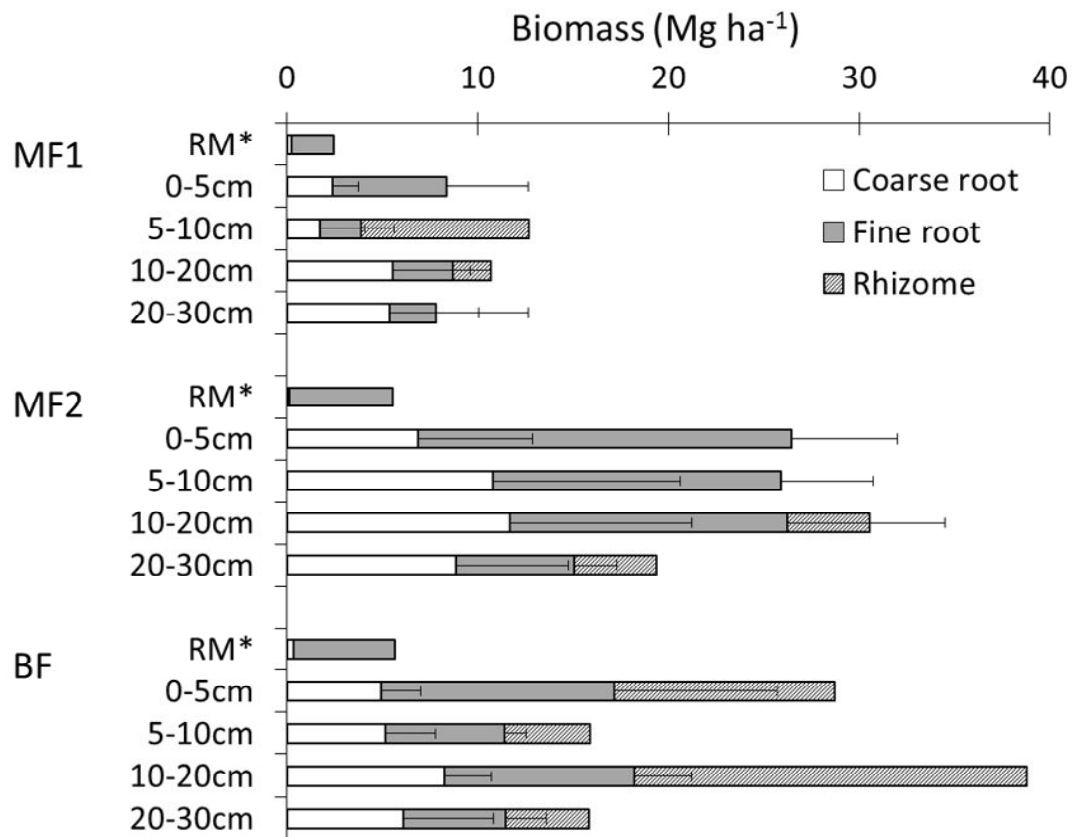
667 Fig. 2



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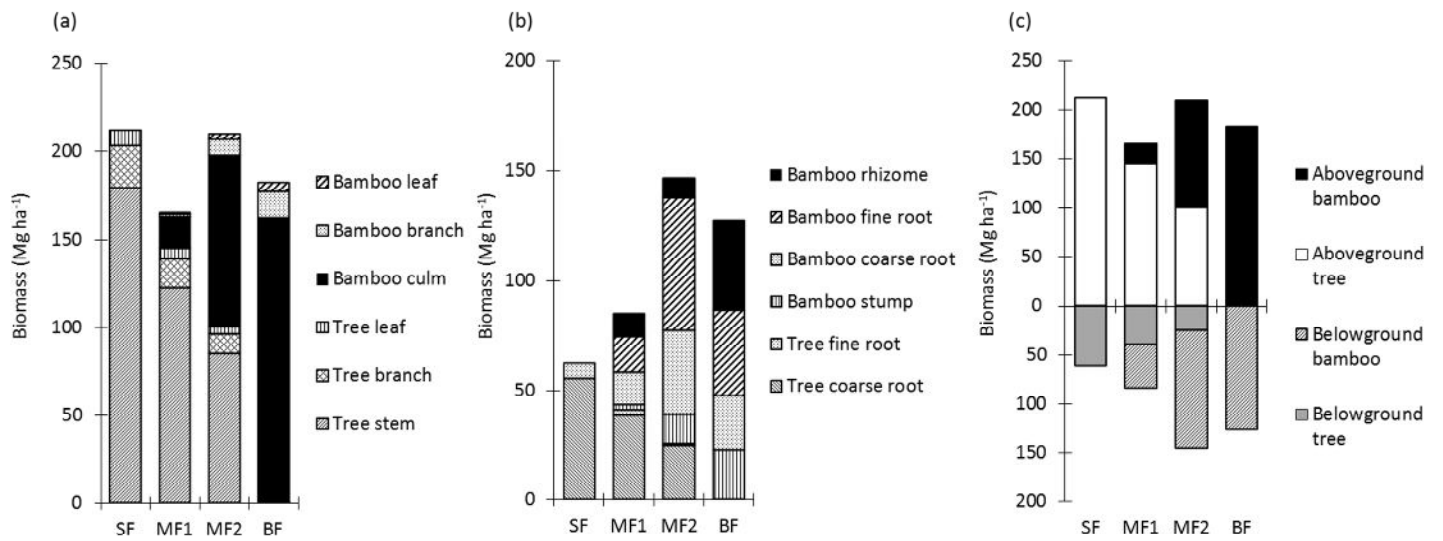
670 Fig. 3



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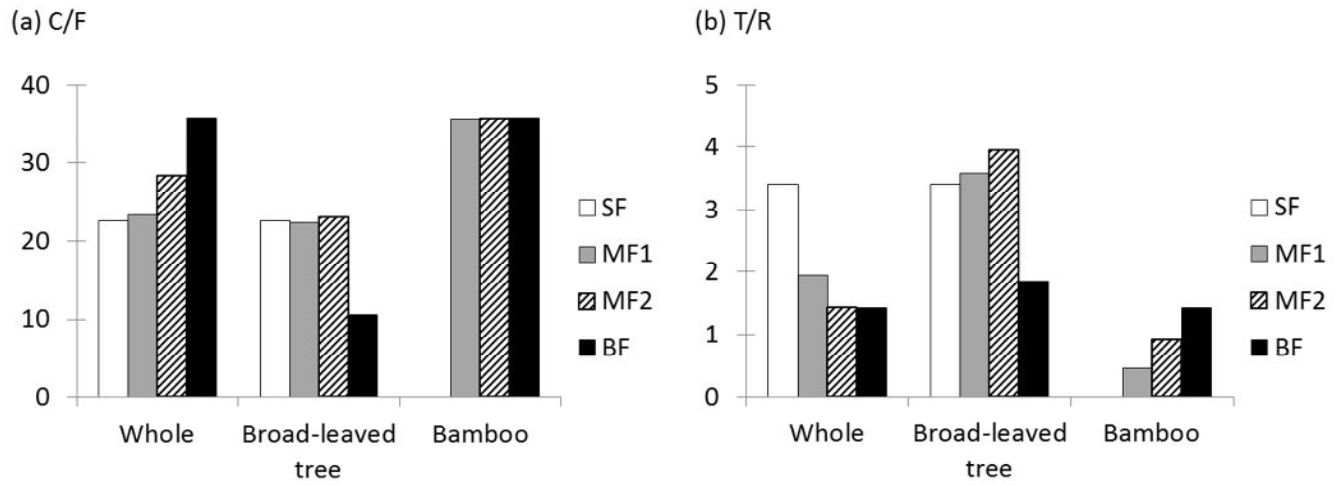
673 Fig. 4



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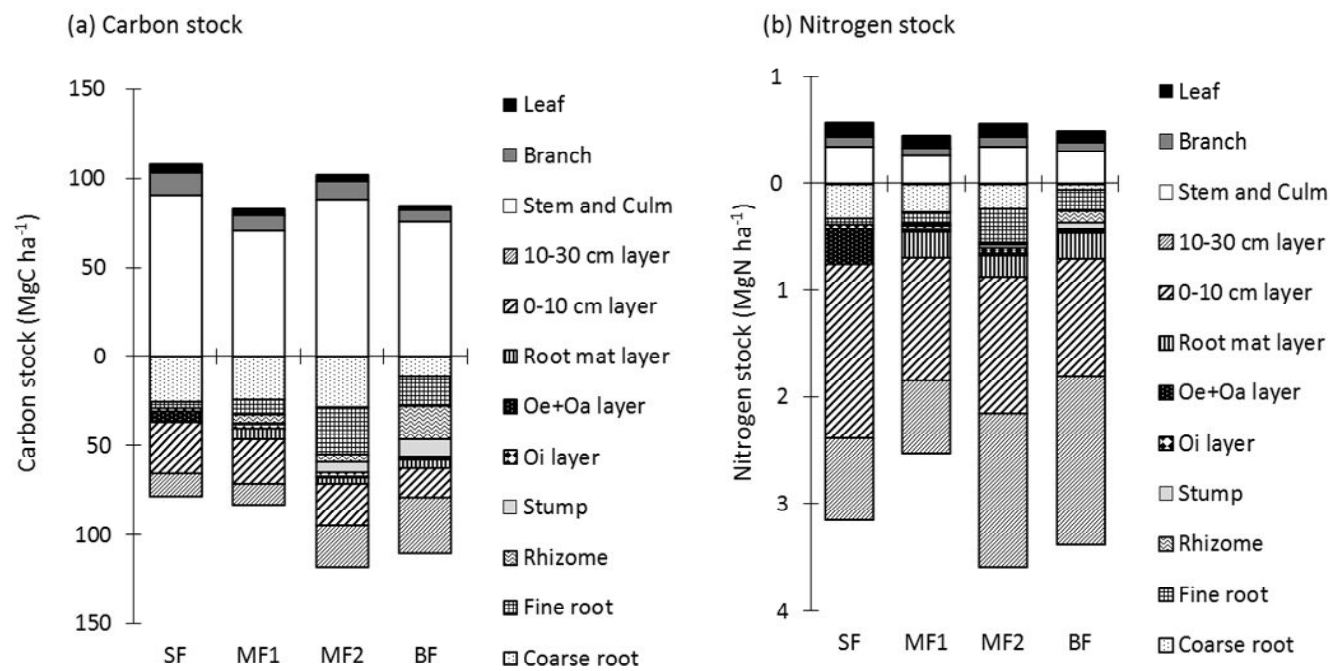
676 Fig. 5



677

678

679 Fig. 6

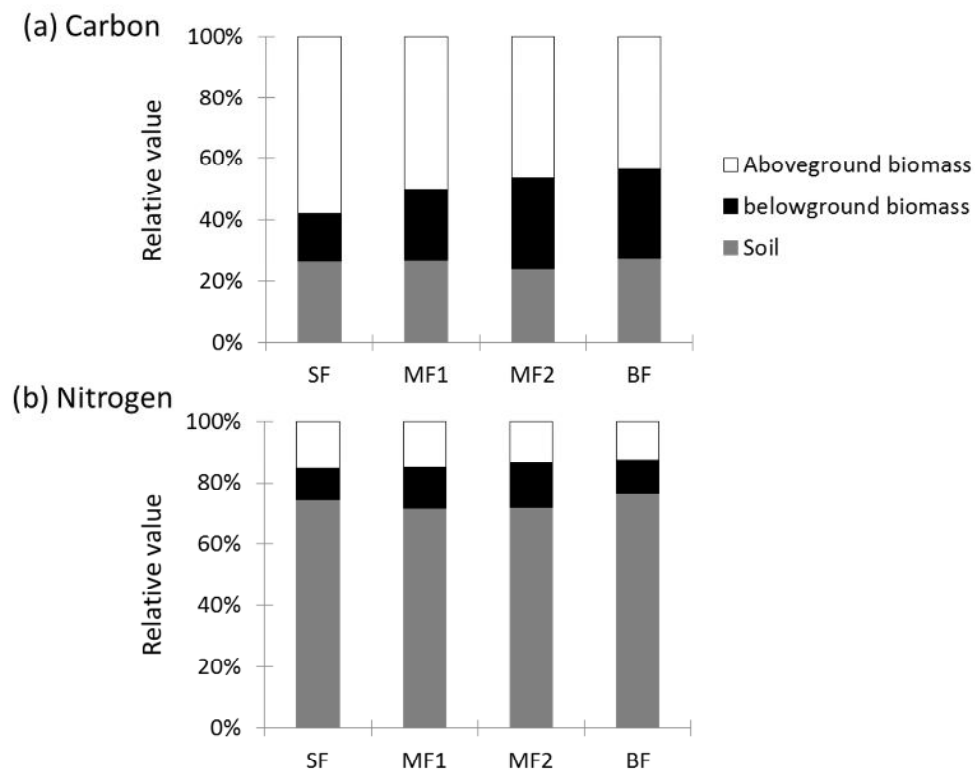


680

681

682

Fig. 7



686 Appendix A. Biomass of above- and belowground compartments, their respective totals, and total values.

687

Mg ha ⁻¹	Broad-leaved tree							Bamboo									Total biomass
	Aboveground				Belowground			Aboveground				Belowground					
	Leaf	Branch	Stem	Total	Coarse root	Fine root	Total	Leaf	Branch	Culm	Total	Stump	Coarse root	Fine root	Rhizome	Total	
SF	8.95	23.8	179.1	211.8	55.2	6.93	62.1	0	0	0	0	0	0	0	0	0	273.9
MF1	6.21	16.4	122.4	145.1	38.3	2.14	40.5	0.54	1.66	17.7	19.9	2.5	15.1	16.0	10.8	44.4	249.8
MF2	4.16	11.2	84.6	100.1	24.3	0.99	25.3	2.98	9.08	97.5	109.6	13.4	38.2	60.8	8.6	121.1	356.1
BF	0.01	0.02	0.07	0.10	0.05	0.00	0.05	4.94	15.1	162.0	182.1	22.3	24.7	39.1	41.0	127.1	309.4

688

689

690 Appendix B. Carbon and nitrogen stocks in aboveground and belowground compartments and in
691 each soil layer, their respective subtotals, and total values.

		SF	MF1	MF2	BF
<i>C (MgC ha⁻¹)</i>					
Aboveground biomass	Leaf	4.7	3.5	3.5	2.1
	Branch	12.3	9.3	10.0	6.9
	Stem and Culm	91.2	70.6	88.7	75.9
	Subtotal	108.2	83.4	102.2	85.0
Belowground biomass	Coarse root	25.5	24.4	28.1	10.9
	Fine root	3.2	7.9	26.7	16.9
	Rhizome	n.a.	4.8	3.8	18.2
	Stump	n.a.	1.1	5.9	9.9
	Subtotal	28.7	38.1	64.6	55.9
Soil	Oi	1.9	1.9	2.3	1.4
	Oe+Oa	5.9	0.5	0.6	0.5
	RM	n.a.	5.5	3.9	4.4
	0-10	29.1	25.3	23.3	16.9
	10-30	12.8	11.8	22.8	30.9
	Subtotal	49.7	45.0	53.0	54.0
Total		186.6	166.5	219.8	194.9
<i>N (MgN ha⁻¹)</i>					
Aboveground biomass	Leaf	0.14	0.11	0.13	0.10
	Branch	0.090	0.071	0.089	0.078
	Stem and Culm	0.34	0.27	0.35	0.31
	Subtotal	0.57	0.44	0.56	0.49
Belowground biomass	Coarse root	0.32	0.26	0.23	0.057
	Fine root	0.053	0.098	0.32	0.20
	Rhizome	n.a.	0.028	0.023	0.11
	Stump	n.a.	0.006	0.035	0.058
	Subtotal	0.38	0.39	0.60	0.42
Soil	Oi	0.041	0.040	0.045	0.022
	Oe+Oa	0.33	0.023	0.023	0.021
	RM	n.a.	0.24	0.20	0.23
	0-10	1.63	1.15	1.28	1.10
	10-30	0.77	0.67	1.44	1.58
	Subtotal	2.77	2.13	2.98	2.96
Total		3.72	2.96	4.15	3.86

692 n.a.: not available.